Communicative & Integrative Biology 4:6, 758-760; November/December 2011; ©2011 Landes Bioscience

Visual input and path stabilization in walking ants

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Key words: navigation, ants, path stabilisation, ocelli, compound eye, *Melophorus bagoti*

Submitted: 08/11/11

Accepted: 08/12/11

DOI: 10.4161/cib.4.6.17730

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Addendum to: Schwarz S, Albert L, Wystrach A, Cheng K. Ocelli contribute to the encoding of celestial compass information in the Australian desert ant *Melophorus bagoti*. J Exp Biol 2011; 214:901–6; PMID:21346116; DOI:10.1242/jeb.049262.

Most animals use vision to navigate the outside world. Eyes are the sensory organs for visual perception and can vary in their form, structure and function to suit the visual requirement of the individual species. In insects, mainly the two compound eyes but also the less-conspicuous ocelli are in charge for visual input. Much knowledge has been obtained about compound eyes but little is known about the role of ocelli in walking insects. Recently it has been shown that ant ocelli contribute to encoding celestial compass information for homing. However, ocelli could not compute terrestrial cues for navigating back to the nest. Here we focus on further investigations on the ants' paths stabilization under different visual input conditions. The pitch and roll stabilization of walking paths seems to be independent of visual input and controlled by idiothetic cues. The yaw (meander) stabilization in walking paths is adjusted for navigational rather than for stabilizing purposes and depends on at least three factors: the odometric component of the path integrator (via idiothetic cues), the perception of the celestial compass information (via ocelli and compound eyes), and the visual matching of the familiar route scenery (via the compound eyes).

For central place foragers, such as ants, it is necessary and important to find the way back to the nest after every foraging trip. To achieve that, some ant species use mainly chemical trails[1,2] but most end up learning their foraging routes independently by relying on visual cues.[3,4] The Australian desert ant *Melophorus bagoti* is one of these solitary foraging ants.[5] While navigating through its cluttered terrain it is mainly guided by idiothetic information and vision based on celestial (e.g., polarized skylight, sun's position) and terrestrial cues (e.g., landmarks, skyline contour).[5] Compound eyes and the three ocelli represent the sensory organs for the visual input. It is known that compound eyes can read celestial compass cues for path integration in ants. They also provide sufficient navigational details of the surrounding landmark panorama for foraging and homing.[6] Far less is known about the function of the ocelli in ants. In flying insects, ocelli detect quickly differences in light gradients and stabilize the gaze and flight via specialized neurons (L-neurons).[7,8] In walking insects however, it has been demonstrated in desert ants that ocelli can encode celestial compass information for navigating back to the nest.[9] Recently, Schwarz et al.[10] tested homing performances of ants with different visual input conditions. The results showed that *M. bagoti* ocelli obtain compass information from celestial cues but cannot encode terrestrial landmark information for homing.

Here we address the role of the visual input in walk stabilization. First, neither compound eyes nor ocelli are necessary for steady walks in ants. Even totally blinded ants could walk readily without any noticeable forward, backward (roll) or sideway (pitch) stumbling and tripping. Thus, it seems that the pitch and roll stabilization in ant paths is independent of the visual input but might be based on sensory input from the legs. In contrast to flying insects, pitch and roll stabilization is directly associated with the ground surface and therefore enables walking insects to receive stabilization information from the moving legs. Most natural surfaces

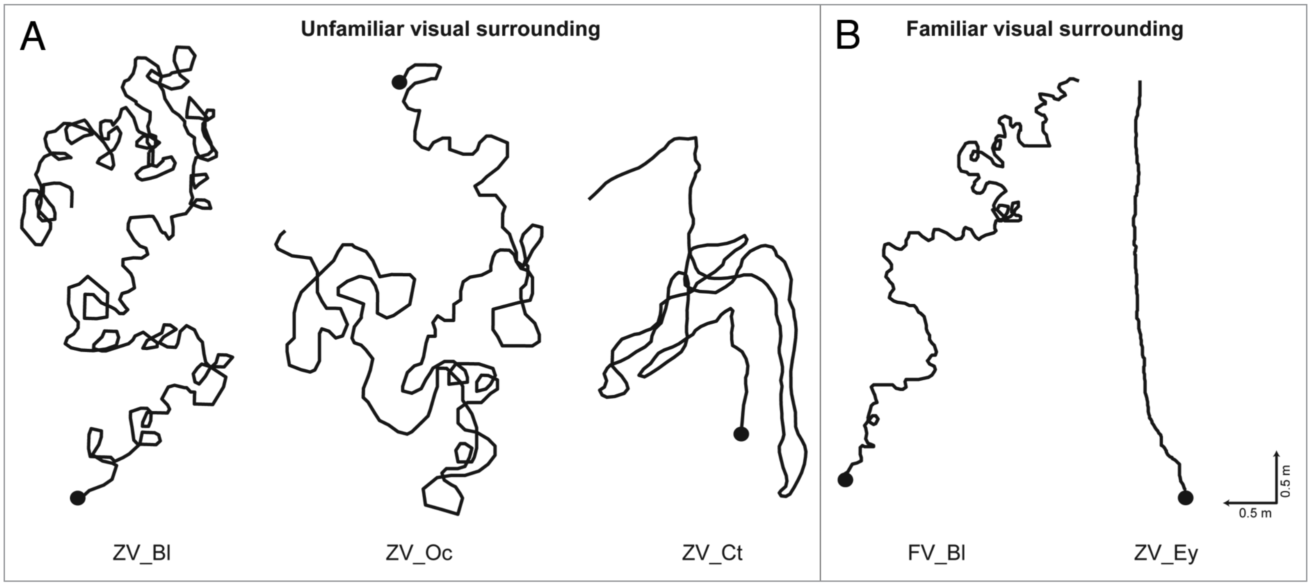

Figure 1. Homing path examples of full-vector (FV) and zero-vector (ZV) ants under different visual input conditions (black dot represents the starting point of the path). (A) Released on unfamiliar grounds, blinded ants (Bl) display paths with the highest meander (yaw angle variation) followed by ants with covered compound eyes but open ocelli (Oc). Ants with untreated eyes (Ct) show stable walks with low meander. (B) FV_Bl ants walk straighter paths than ZV_Bl ants from part (A). The odometric component of the path integrator, via idiothetic cues, leads to a less meanderous path. Released on familiar grounds, ZV ants with uncovered compound eyes (Ey) stabilize their yaw angle by using the familiar scenery and perform paths with the lowest meander among all experimental groups.

are uneven or rugged. In order to keep a proper roll and pitch position it seems plausible to rely on the direct information of the legs rather than on an absolute pitch and roll stabilization relative to the visual scenery, which would lead to complications in walks on uneven grounds.

What about the yaw stabilization or the level of meander in walking ants? On the one hand we analyzed the yaw angle of ant walks with no information from the path integrator (zero-vector, ZV) when released on unfamiliar grounds. All tested ants started moving activity but totally blinded ants (**Fig. 1A**, Bl) displayed paths with the highest meander,[10] which leads to the conclusion that visual input is heavily involved in yaw stabilization. Ants with covered compound eyes but open ocelli (**Fig. 1A**, Oc) showed lower meander levels in their walks.[10] Thus, ocelli play a little role in controlling the yaw angle. The gain in yaw stability might result from the ability of ocelli to read celestial compass cues. Additional visual input from the compound eyes (**Fig. 1A**, Ct) decreased the meander and therefore increased the yaw stabilization of the ant walks. This could be due to a combination of celestial compass information perceived by the dorsal rim area of the compound eyes or the perception of terrestrial landmarks although neither information from the path integrator nor the familiarity of the surrounding were available under this experimental condition.

On the other hand we analyzed the yaw angle of ant paths with the full information from the path integrator (full-vector, FV) when released on unfamiliar grounds. Totally blind ants, ants with ocelli only and ants with compound eyes and ocelli all showed a lower meander as FV ants than as ZV ants.[10,11] Information about the distance and direction from the path integrator induces straighter walks. Remarkably, the difference between ZV and FV blind ants (**Fig. 1A and B**, Bl) even reveals that visual cues are not necessary for lowering the meander, implying that the yaw stabilization in walks is also controlled by idiothetic information. It suggests that the odometric component of the path integrator influences the ants' walking behavior—even without visual input.

We also investigated the yaw angle of ZV ant paths in familiar visual scenery. The focus lies on ants with open compound eyes and covered ocelli (Ey) since blind ants and ants with ocelli only cannot compute terrestrial landmark information.[10] ZV_Ey ants lacked any information from the path integrator but displayed walks with the lowest meander among all test conditions (**Fig. 1B**, Ey).[10] It appears that the familiar visual surrounding provides the best information for yaw angle stabilization but only if the match between the current and memorised view is sufficiently correct (**Fig. 1B**, Ey). Indeed, when ants are displaced several meters from their foraging route, they performed fairly meanderous walking paths although the scenery is familiar enough to lead them toward their well-known route corridor.[12] Paths become only very straight when ants hit their familiar route corridor. This might be due to a particular view-based strategy which consist in aligning the body as to match the features on memorised and current views.[13,14] This phenomenon can be called using a visual compass and provides a non-ambiguous direction for travel on a familiar route.[15-17] The yaw stabilization on familiar routes seems to be further improved when the direction of travel is in synergy with the direction dictated by the path integrator.[14] This suggests that odometric information, perception of celestial compass cues and matching of the familiar scenery need to be in congruence to output the straightest path.

In conclusion, we want to point out that contrary to flying insects,[7] pitch and roll stabilization in ground-based insects seems to be controlled by idiothetic rather than visual cues. In walking insects ocelli are not crucial for movement stability but help to maintain lower variation in yaw angles by providing celestial compass information. The straightness of the path in pedestrian ants depends on at least three factors: the odometric component of the path integrator (via idiothetic cues), the perception of the celestial compass (via ocelli and likely the compound eyes), and most importantly, the visual matching of the familiar route scenery (via the compound eyes). These factors act in synergy to produce straighter paths in certain navigational contexts and more meander in uncertain or conflicting navigational contexts. Thus, in walking ants, the maintenance of a stable yaw angle is mostly adjusted for navigational purposes, and not for stability purposes.

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